

PN-A&K-397
75449

Ann. Rev. Ecol. Syst. 1986. 17:1-16
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SOIL-PLANT RELATIONSHIPS IN THE TROPICS

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INTRODUCTION

As commonly defined, the tropics comprise that region of the earth lying between the Tropics of Cancer and Capricorn, constituting 38% of the land surface (5×10^9 ha). The tropics may also be defined as those areas with mean temperatures greater than 18°C in all months of the year. A third definition of the tropics specifies those areas with soils in which the temperature at a depth of 50 cm varies less than 5°C between summer and winter (39). Compared to the geographical definition, these latter definitions reduce the area considered to be tropical. In contrast to the temperate region where low temperature restricts plant growth at some period of the year, in the tropical regions the length of the growing season is determined by the amount of rainfall and its temporal distribution. Dudal (13) has separated the tropics into five major ecological zones based on growing periods: humid, subhumid, semiarid, arid, and wetland. The growing season varies from 12 months in the humid zone to nearly 0 months in the arid regions. In the tropics a wide range of climate and vegetation exists, owing mainly to variations in amount and duration of rainfall.

SOIL CHARACTERISTICS

There is no uniquely tropical soil, just as there is no uniquely temperate soil. Tropical soils of the world vary in their properties at least as widely as do those soils found in other regions.

Within the past two decades a system of soil taxonomy has been developed by the Soil Survey staff of the US Department of Agriculture (39); in this

system, soils are grouped and named according to their measurable properties. The system contains 6 categories in a hierarchical relationship in which the number of classes increases as rank decreases.

We will consider separations only at the highest level, the order, of which there are 10. Here the classes are distinguished on the basic properties that mark soil-forming processes on the grand scale. It is interesting that only in the tropical regions of the world are all 10 orders found. In fact, soils of all 10 orders can be found on the island of Puerto Rico. In our consideration of plant nutrition in the tropics, we will confine our discussion to three orders: Alfisols, Ultisols, and Oxisols. Alfisols include about 800×10^6 ha, Ultisols 600×10^6 ha, and Oxisols 1100×10^6 ha. These 3 orders constitute about 50% of the land area of the tropics. We are excluding the rice growing areas from our discussion because rice nutrition requires a very special set of soil and growing conditions. The soil orders we consider are those in which most of the food crops are grown or on which subsistence farming occurs in the tropical regions.

The Alfisols are characterized by a subsoil horizon of increased clay content (argillic) with base saturation greater than 35% or in which the base status increases with depth. According to Aubert & Tavernier (2), Alfisols typically occur in the transitional zone between humid and arid climates. Two main suborders occur in tropical regions: Udalfs have only short periods when the soil is dry, while Ustalfs have long periods when the soil is dry (more than 90 days cumulative). Most of the Alfisols of the tropics fall into the suborder Ustalfs. Alfisols of West Africa studied by Moorman et al (28) and Gallez et al (17) have well-developed argillic B horizons and modest cation retention capacity [5–10 cmol(p⁺) kg⁻¹ soil in the surface horizons]; also, 90% or more of cation retention capacity is satisfied by Ca²⁺ and Mg²⁺ throughout the soil profile (Table 1). Soil acidity is not a problem in these soils nor is a shortage of Ca²⁺ or Mg²⁺. The clay-sized fraction of tropical, as opposed to temper-

ate, Alfisols is dominated by kaolinite and contains smaller amounts of goethite and hematite—an indication of intense weathering in the past. These profiles usually contain small amounts of micas and other weatherable minerals. Since the exchangeable cations are largely Ca²⁺ and Mg²⁺, these soils must have been recharged with bases in the recent past. Thus, these soils fall into the more productive high-base-status soils described by Sanchez & Buol (37).

The Ultisols, found characteristically under forest vegetation, also have an argillic subsoil horizon. In contrast to the Alfisols, however, these soils have a low supply of bases, particularly in the lower horizons. In addition, they are limited to areas where the mean annual soil temperature is more than 8°C. In a group of Ultisols studied by Sanchez & Buol (36), the clay fraction was dominated by kaolinite but also contained detectable quantities of less weathered minerals. The cation retention capacity of these soils is low [3–10 cmol(p⁺) kg⁻¹ soil], but not greatly different from that of the Alfisols (Table 2). The Ultisols, however, are highly acid throughout the profile, and the dominant cation on the exchange complex is neutral salt extractable Al³⁺ (upwards of 90% of the exchangeable cations). Much of the Ca²⁺ and Mg²⁺ in these profiles is found in the surface horizon, to which it presumably has been cycled by the forest vegetation.

The Oxisols are the only soil order that occurs exclusively in the tropics. These soils are characterized by an oxic horizon in which the clay fraction is dominated by kaolinite and/or gibbsite. Amorphous materials occur in many profiles. The capacity of these soils to retain cations is very low [≤ 3 cmol(p⁺) kg⁻¹ soil, or less], and the subsoil horizons of many of these soils are essentially devoid of plant nutrients, especially Ca²⁺ (Table 3). Much of the cation retention capacity is due to the organic matter found largely in the surface horizon. While Al³⁺ is the dominant cation on the exchange complex, the absolute amount is small compared to that found in the Ultisols because the cation retention capacity is so low.

Table 1 Physical and Chemical Properties of an Alfisol from Nigeria*

Horizon	Depth (cm)	Physical properties			Chemical properties					
		Sand (%)	Silt (%)	Clay (%)	pH	Adsorbed				CEC
						Al	Ca	Mg	K	
						[cmol (p ⁺) kg ⁻¹ soil]				
A1	0–18	66	13	21	6.5	0.07	6.7	1.8	0.3	9.3
E3	18–36	70	11	19	6.9	0.06	2.5	1.2	0.2	4.5
B21	36–65	54	14	32	6.5	0.04	3.9	1.4	0.3	6.0
B22	65–87	43	14	43	6.2	0.08	6.1	2.5	0.2	9.4
B3t	87–127	35	18	47	6.2	0.08	6.1	2.5	0.2	9.4
C1	127–187	47	23	30	6.0	0.06	6.1	4.0	0.1	10.9

*From Ref. 28.

Table 2 Physical and Chemical Properties of an Ultisol from Peru*

Horizon	Depth (cm)	Physical properties			Chemical properties					
		Sand (%)	Silt (%)	Clay (%)	pH	Adsorbed				CEC
						Al	Ca	Mg	K	
						[cmol p ⁺ kg ⁻¹ soil]				
A1	0–5	60	28	12	3.6	1.9	1.0	0.4	0.3	3.6
E21	5–40	44	36	20	4.2	4.2	0.2	0.1	0.2	4.7
E22	40–60	48	28	24	4.1	4.5	0.4	0.1	1.2	5.2
B1	61–90	40	36	24	4.2	6.0	0.2	0.1	0.2	6.5
B2	90–140*	44	26	30	4.0	6.1	0.2	0.1	1.9	8.4

*From Ref. 36.

Table 3 Physical and Chemical Properties of an Oxisol from Brazil*

Horizon	Depth (cm)	Physical properties			Chemical properties			
		Sand (%)	Silt (%)	Clay (%)	pH	Adsorbed		
						Al [cmol (p+) kg ⁻¹ soil]	Ca & Mg kg ⁻¹ soil]	K CEC
Ap	0-10	36	19	45	4.9	1.9	0.4	0.1
E3	10-35	33	19	48	4.8	2.0	0.2	0.05
B1	35-70	35	18	47	4.9	1.6	0.2	0.03
B21	70-150	35	18	47	5.0	1.5	0.2	0.01
B22	150-260	39	10	42	4.6	0.7	0.2	0.02

*From Ref. 15.

It is significant that the clay fraction of these soils, which is dominated by kaolinite and hydrous oxides, has very little permanent negative charge, and this results in a very low cation retention capacity within the pH range found under natural conditions. The magnitude and the sign of the surface charge of these minerals are dependent upon the pH and the nature and concentration of the electrolyte in solution (42). Such clay fractions are characterized by surfaces that have a constant surface potential determined solely by the quantity of potential determining ions, H^+ and OH^- . The resultant net surface charge is determined by the ratio of H^+ to OH^- ; the charge reduces to zero (zero point of charge or ZPC) when equal amounts of the charged species are present. The cation retention capacity of the soil is highly variable. At highly acidic soil pH (typical of many of these soils), the net negative charge and effective cation retention capacities are very low. Gallez et al (16) showed that the ZPC of subsoils they tested fell in the following order: Alfisols < Ultisols < Oxisols, with average pH values of 3.5, 4.0, and 5.5, respectively. The subsoils of some Brazilian oxisols had cation retention capacities less than 2 cmol(p⁺) kg⁻¹ of soil. Plant nutrition problems in these soils are severe because the supply of essential cations is so low.

Common procedures for determination of cation retention—with salt solutions at a specified pH value, usually 7 or 8—are adequate when the cation retention capacity is dominated by a permanent negative charge, such as is found in smectites or vermiculites. With the highly weathered soils, however, the distribution of electric charges, as well as the ZPC, can best be determined by equilibrating the soils with a dilute salt solution such as $CaCl_2$ at several pH values and then by measuring the adsorption of both Ca^{2+} and Cl^- . Such a procedure (16, 42) is theoretically sound and reflects more accurately than the buffered salt solutions the development of electric charges and the cation and anion retention capacities of these soils. The total supply and availability of the essential cations for plants that are contained in these highly weathered soils can be predicted more reliably by this procedure.

SOIL ACIDITY AND CALCIUM NUTRITION

The Alfisols of the tropics are usually well supplied with Ca^{2+} and Mg^{2+} throughout the soil profile. The Ultisols and Oxisols are extremely acid throughout the soil profile, and generally Oxisols contain extremely small quantities of Ca^{2+} , especially in the subsoil. Much of the early research on soil acidity was done to understand factors that were deleterious to growth of plants, particularly crop plants on acid soils. Arnon & Johnson (1) demonstrated that many plants grew satisfactorily in solutions which ranged in pH from 4 to 8, provided precautions were taken to eliminate harmful secondary effects. Schmehl et al (38) showed that 10 ppm Al^{3+} in solution reduced Ca^{2+} uptake to one tenth of that found in control plants, whereas 100 ppm of Al^{3+} in solution virtually inhibited the uptake of Ca^{2+} by alfalfa plants. They concluded that the deleterious effects of acid soils on plant growth were due to high levels of Al^{3+} in the soil solution.

Brenes & Pearson (8) showed that Al^{3+} in solution restricted root growth of maize and sorghum but did not detrimentally affect stargrass roots. Sorghum root growth dropped sharply with the first increment of soil solution Al^{3+} (>0.0009 mM). About twice as much solution Al^{3+} was required to bring about the same reduction in root growth of maize. They found no difference in root growth within either species when grown on either an Ultisol or an Oxisol if the soil solution Al^{3+} level was the same. They concluded that root inhibition in acid humid-tropical soils was primarily a result of soil solution Al^{3+} toxicity. There were, however, large differences in response of the three species they tested. They concluded from their analyses of the soil solution that Ca^{2+} should be adequate for plant growth even in the most acid soils. Blarney et al (4), using solution culture studies, have shown that soybean root elongation was best correlated with monomeric forms of Al in solution and not necessarily with total Al in solution. It seems likely that most of the monomeric Al was Al^{3+} . The solution chemistry of Al is complex, and determination of the concentrations of the ion species in solution is essential for interpretation of the results of studies of Al toxicity. Working on Ultisols of the southeastern United States, Kamprath (22) showed that the soil content of exchangeable Al^{3+} (extracted by an unbuffered neutral salt solution) correlated best with poor growth of plants. In these Ultisols, the content of exchangeable Ca^{2+} was sufficiently great that Ca^{2+} supply did not limit plant growth.

In contrast to the Ultisols, many of the Oxisols contain very small quantities of both exchangeable Ca^{2+} and Al^{3+} , particularly in the subsoils. Subsoils with less than 0.02–0.05 cmol(p⁺) kg⁻¹ of exchangeable Ca^{2+} have been reported. Even in the absence of toxic quantities of Al^{3+} , root growth into these subsoils is severely limited. The net result is that plant roots are

concentrated in the surface horizon and plants have an increased vulnerability to water stress. Work by Ritchey et al (35) has clearly demonstrated that soybean roots did not penetrate below 60 cm where the Ca^{2+} content of the soil was less than $0.025 \text{ cmol(p}^+) \text{ kg}^{-1}$ soil; these plants therefore suffered from water stress after 17 days without rain. In a nearby site where the Ca^{2+} content of the subsoil was higher, plants were able to extract water from deeper depths and wilting did not occur. Ritchey et al (34) also demonstrated that the addition of small quantities of Ca^{2+} to the rooting medium [$0.21 \text{ cmol(p}^+) \text{ kg}^{-1}$ soil] resulted in root elongation in a soil free of exchangeable Al^{3+} . Calcium is not translocated within the plant toward the growing root tip, at least not in annual plants (7). Therefore, the Ca^{2+} required for root growth must be taken from that soil immediately adjacent to the root.

The Al^{3+} in solution reduces root growth even in the presence of otherwise adequate Ca^{2+} . Bohnen (5) studied the influence of Ca^{2+} , Al^{3+} , and pH in solution on the growth of maize in two inbred lines. With both inbreds at solution pH 5, one ppm Ca^{2+} with no Al^{3+} was sufficient for maximum root elongation. At a lower pH, one inbred required a higher Ca^{2+} level to obtain the same rate of root growth as at pH 5, while the second was less affected. While attempting to determine mechanisms of Al^{3+} toxicity, Bohnen showed that maize roots had a greater Al^{3+} concentration in the cytoplasm than in cell walls and greater Al^{3+} concentration in the epidermis and cortex than in the stele. A few hours exposure to Al^{3+} in solution caused rupture of the cell walls and loss of cellular material through the epidermis. In susceptible plants, normal uptake of ions from soil solution would thus be disturbed, and the plant would grow poorly.

Kirlew (24) measured changes in pH, Ca^{2+} , and Al^{3+} levels in the rhizosphere of several maize inbreds and hybrids. He found that the pH of the rhizosphere soil samples was lower than that of the bulk soil sample. He also found that the rhizosphere soil contained more KCl-extractable Al^{3+} , less KCl-extractable Ca^{2+} , slightly more water soluble Ca^{2+} , and less total Ca^{2+} than the bulk sample. His results are consistent with the hypothesis that Ca^{2+} uptake depletes Ca^{2+} in the rhizosphere and that H^+ is released by the root in response to greater uptake of cations than anions. This in turn results in dissolution of basic Al compounds and increased KCl-extractable Al^{3+} .

That various plant species and varieties within species vary in their tolerance to Al^{3+} in soil solution is certain. Brenes & Pearson (8) showed that in the presence of adequate Ca^{2+} , root growth of stargrass was not affected at pH 4 nor at the highest Al^{3+} concentration, whereas the root growth of both maize and sorghum was drastically reduced. Some tropical grasses grow well at relatively low levels of Ca^{2+} saturation and high levels of Al^{3+} saturation (23). Even in the presence of high Al^{3+} saturation, uptake of Ca^{2+} appears adequate. With 4–6 g $\text{Ca}^{2+} \text{ kg}^{-1}$ of plant material, the result was reasonable

plant growth. Using a novel 4-day assay Ritchey et al (35) were able to separate Al^{3+} toxicity from Ca^{2+} deficiency in a number of maize and sorghum lines developed in Brazil. For Al^{3+} -sensitive plants, root growth was seriously restricted in subsoils with high Al^{3+} contents and Ca^{2+} levels well above the critical range. For Al-tolerant lines and in Al^{3+} -free subsoil, decreased root growth was due to inadequate Ca^{2+} . In Ca^{2+} -deficient subsoil, maize root length was only one fourth that seen when $0.08 \text{ cmol(p}^+) \text{ as Ca}^{2+} \text{ kg}^{-1}$ of soil was added.

It is clear that many Ultisols and some Oxisols contain sufficient quantities of Al^{3+} to limit dry matter accumulation of many plants growing on these soils. Probably Al^{3+} interferes with normal root elongation and function and thus limits growth. Unequivocal evidence also exists to show that the Ca^{2+} content of many Oxisols is insufficient to permit normal root growth even in the absence of toxic levels of Al^{3+} . Thus, to enhance root growth particularly into the subsoils, additional Ca^{2+} must be supplied. On these soils, much of the native vegetation has rooting restricted to the surface layer of the soil. As a consequence, subsoil water does not contribute to plant growth. Plant nutrients found in subsoil horizons are not taken up by plants, and recycling of these essential elements is likewise limited.

PLANT GROWTH AND PRODUCTION

There is virtually no direct evidence that native terrestrial ecosystems are nutrient limited. Jordan & Herrera (21) used correlation analyses to conclude that soil Ca^{2+} concentration was a reliable index of potentially limiting nutrients. Vitousek (44) concluded from his analyses of data in the literature that P but not N commonly limited production of tropical rain forests. The de Wit group (10) used fertilization experiments in native grasslands of the Sahel and demonstrated N and P limitation. Presumptive evidence of nutrient limitation results from experiments in which native ecosystems have been converted to agricultural production. Additions of P and/or N invariably increased productivity. It is extremely difficult to demonstrate nutrient limitations without disrupting the native ecosystem. A procedure described by de Wit & Penning de Vries (10) involves an elegant yet simple model of plant production which result from increasingly severe limitations to plant productivity. De Wit developed the concept of systems at different levels of production as an outgrowth of his analyses of constraints to production of agricultural crops. As these constraints result from the effects of external factors on physiological processes, they apply to plant growth and production generally. Heterogeneity makes analyses of natural systems more difficult

than that of derived systems, but it certainly does not preclude the possibility of using de Wit's definitions of production levels.

Production Level 1

Plant growth takes place with ample supplies of plant nutrients and water. Growth rate and dry matter accumulation are limited by weather conditions. This situation may be realized in well-managed agronomic field experiments and in glass houses where growth rate amounts to 100–350 kg dry matter $\text{ha}^{-1} \text{day}^{-1}$. According to Penning de Vries (30), the major elements of this system are dry weight of leaves, stems, and reproductive or storage organs; the major processes are photosynthesis, growth and maintenance, biomass distribution, and leaf area development.

Production Level 2

Plant growth is limited by water during some portion of the growing season. This occurs on soils well supplied with nutrients. The additional elements of this class of systems are the plant and soil water balances; the important process is transpiration.

Production Level 3

Plant production is limited by nitrogen. This situation is common in agricultural and natural systems where inputs of nitrogen are limited. Important components of this system are nitrogen in the soil and in the plant. The important processes are transformations of soil nitrogen, absorption by the roots, growth-availability interactions, and redistribution within the plant.

Production Level 4

Plant production is limited by the availability of phosphorus. Observed growth rates vary from 10–50 kg dry matter $\text{ha}^{-1} \text{day}^{-1}$ over a growing season of about 100 days. Important elements of this system are the nitrogen and phosphorus contents of the soil and the plant. The important processes are their transformations in the soil, absorption by plant roots, and plant growth response to their availabilities.

It is likely rare to find a system that fits into Production Level 1, where growth and dry matter accumulation are limited only by weather conditions. Some of the intensively managed forage crops reported by Vicente-Chandler (43) achieved very high growth rates over an extended period of time. This was accomplished by intensive fertilization, especially with nitrogen, and by management of cutting that resulted in dry matter accumulation approaching 350 kg $\text{ha}^{-1} \text{day}^{-1}$, at least over some portion of the closed-canopy, linear-growth phase between cuttings. A growth rate of sugar cane of 300 kg dry matter $\text{ha}^{-1} \text{day}^{-1}$ can be maintained over a full year. According to de Wit et

al (11), potential production rates of C_4 plants range from about 350 kg to about 200 kg dry matter $\text{ha}^{-1} \text{day}^{-1}$. For C_3 plants, most of which are found in temperate regions, the potential production rate is about 200 kg dry matter $\text{ha}^{-1} \text{day}^{-1}$.

In many tropical ecosystems the standing biomass is large. The rate of accumulation in these systems, however, may be much less. Nye & Greenland (29) showed that maximum rates of dry matter accumulation under forest were of the same order as those for managed systems during the early growth stages. The mean annual increase in nutrient storage in the vegetation during the first 5 years of the growth period was double that of the first 18 years or the first 40 years. Dry matter accumulation was about 15,000 kg $\text{ha}^{-1} \text{yr}^{-1}$ in the first 5 years and about 7,000 kg $\text{ha}^{-1} \text{yr}^{-1}$ over the first 18 years. It seems likely that these systems were nutrient limited and possibly water limited over the entire growth period.

Penning de Vries (30) considers that the water limitation of plant growth (Production Level 2) is uncommon. We believe, however, that water limitation combined with a hostile root environment results in decreased plant productivity. In the cerrado regions of Brazil the probability of water deficit at some time during the growing season is high. Bouldin (6) in his summary of the work done by our group in Puerto Rico and Brazil showed clearly that a sufficiently long period without rain, enough to reduce plant growth, occurred nearly every year. This was especially evident with those crop plants sensitive to soil acidity, where rooting was restricted to the treated surface horizon. Incorporation of lime into the subsoil allowed root growth into a larger volume of soil, and this resulted in greater water extraction and greater grain yield of maize. Bandy (3) demonstrated that neutralization of subsoil acidity, which in turn allowed maize roots to penetrate to greater depths, reduced the internal water stress of the plant and reduced stomatal resistance. The plant was thus allowed to transpire and take up CO_2 . In his experiments, Bandy found that a 10–15 day period of water stress during the grain formation stage decreased grain yields by 100–150 kg $\text{ha}^{-1} \text{day}^{-1}$ of stress. Water stress during the vegetative stage reduced plant size, but grain yield was not substantially reduced.

Similar effects on natural systems are not well documented. Goodland & Pollard (19) noted that during the dry season, tree leaves in cerrado remained greener than those in cerrado, presumably because of better soil-water supply. Eiten (14) suggests that cerrado forest is more likely to establish on soils with higher water-retention capacity, and cerrado on soils with lower water-holding capacity. Dense gallery forests are also common along streams within the Brazilian cerrado where the water table is closer to the surface. Separating effects of soil-water supply and soil fertility in cerrado communities is difficult, and interactions are likely to be involved in determining community

composition and production. In the Brazilian cerrado, reduction of plant production by water stress and a hostile root environment is at least as great as is the effect of nutrient stress. These may be more common in other regions than is usually believed, especially where rooting depth is limited by acidity or other hostile factors.

In a series of experiments on pasture production in the Sahel, Penning de Vries & van Keulen (32) demonstrated a classic example of Production Level 3, nitrogen limitation, where conventional wisdom indicated that the system was water limited. The production of native vegetation, mostly annuals, in the rainfall zone of 500 mm was about 2,000 kg ha⁻¹. With optimal water supply, production was about 5,000 kg ha⁻¹. With natural rainfall, but with an optimum supply of nitrogen and phosphorus, dry matter production increased to nearly 10,000 kg ha⁻¹. In these native systems the nitrogen input from all sources—rainfall, legumes, and soil organic nitrogen mineralization—was in the range of 10–20 kg ha⁻¹. At minimum nitrogen content, 5 g kg⁻¹ of plant material, the potential quantity of dry matter production was 2,000–4,000 kg ha⁻¹. The amount of dry matter produced in most of their experiments without nitrogen addition was about 2,000 kg ha⁻¹. Additions of 100–150 kg fertilizer nitrogen ha⁻¹ increased dry matter production to about 8,500 kg ha⁻¹. No vegetation grew in native systems during the very long dry season. During the rainy season, effective water utilization by growing vegetation was no more than 20% of total rainfall. When constraints caused by nitrogen and phosphorus shortage were removed, transpiration increased to about 50% of total rainfall. Most of the natural vegetation consists of C₄ plant species, the rate of growth of which under optimal conditions of nutrients and soil moisture is about 200 kg ha⁻¹ day⁻¹. In contrast, the growth rate of these nutrient limited systems during the growing season was about 30–35 kg ha⁻¹ day⁻¹.

Although annual productivity of the soils of the Sahel is more commonly limited by nitrogen than by phosphorus, some soils fall into Production Level 4, where phosphorus is most limiting. The soils of the cerrado of Brazil are always severely phosphorus limited. With maize, for example, so little phosphorus is available in these soils that once the seed supply is exhausted, no further growth occurs and the plants die (25, 45). These soils in their native state are the most deficient in phosphorus we have ever seen. Crop plants fail completely when planted without fertilizer phosphorus. Normal plant growth occurs, however, and maize grain yields exceeding 6,000 kg ha⁻¹ are obtained on a continuing basis when adequate phosphorus is supplied. These soils are high in Fe and Al oxides, which react with large quantities of fertilizer phosphorus; even so, the availability of phosphorus remains high for extended periods of time. There is a significant native vegetational gradient formed in the Brazilian cerrado (18); the gradient ranges from herbaceous

vegetation with scattered scrub trees to a cerrado or woodland with a dense canopy. Goodland & Pollard (19) related these differences to a soil fertility gradient of N, P, and K. Although he found no relationship between basal area of trees and soil acidity factors, Goodland did conclude that cerrado plants had to be extraordinarily tolerant of Al³⁺. Lopes & Cox (26) found similar relationships between vegetation and soil P and K concentration. In addition, they found positive correlations among the density of woody vegetation and soil pH, exchangeable Ca²⁺, and exchangeable Mg²⁺. Aluminum saturation also appears to affect composition of the plant community. In an interesting study of cerrado vegetation, Peres et al (33) found litter fall of 2,100 kg ha⁻¹ under cerrado and 7,800 kg ha⁻¹ under cerrado. Goodland (18) earlier suggested that this difference of litter production was likely due to differences in fertility. Peres et al (32) showed that the nutrient concentration of the litter from the two sites was not different. The phosphorus concentration averaged 0.6 g kg⁻¹ of plant material, which is extremely low. Nitrogen concentration was 8 g kg⁻¹ of plant material. Litter disappearance rates were about 7% under cerrado and about 15% under cerrado. In cerrado, litter fall contained about 1.25 kg phosphorus of which 0.2 kg cycled annually. Under the cerrado vegetation, comparable figures were 4.7 kg total and 0.3 kg P cycled annually. If 0.2 and 0.3 kg phosphorus are reasonable estimates of available phosphorus in these soils, it is little wonder that crop plants fail without fertilizer phosphorus. Our experience indicates that this is a generous estimate of the phosphorus available to plants.

In practice, it is important to determine whether plant growth occurs at Level 3 or 4. Once the principal growth limiting factor has been established, work can focus on this factor to the exclusion of those that are not important. Penning de Vries et al (31) suggest that the P/N ratio in the plant tissue is of particular importance in determining which element is the principal growth limiting factor. Dijkshoorn & Lampe (12) showed that N and P are functionally related in the plant, and the P/N ratio in sunflowers fell between about 0.04 and 0.15 regardless of the P/N ratio in solution. The P/N range in other species was not greatly different. Based on their experiments, Penning de Vries et al (31) concluded that when the P/N ratio of an annual plant is about 0.04 g P g⁻¹ organic N, the plant is highly P deficient. P additions will increase plant growth, while N additions will not enhance productivity until the former deficiency is corrected. Conversely, when the P/N ratio approaches 0.15, P additions will have no effect, while N additions will be effective. When the P/N ratio approaches one of these limiting values, plant growth will be severely retarded. Using the analyses of Peres et al (33), we calculated the P/N ratio of 0.07 for both the cerrado and the cerrado vegetation. With maize on the cerrado Oxisol, Yost (45) found that P/N ratios approached 0.04 when fertilizer P sufficient to produce about 20% of max-

imum yield was applied. As noted previously, some fertilizer P had to be applied to achieve any measurable growth. We know of no data from natural systems that show severe N deficiencies in the presence of adequate P as P/N ratios approach 0.15. More often, the situation is such that the P/N ratio of plant tissue is in midrange, and both N and P uptake are limited because availability is low. Penning de Vries et al (31) admit that well-fertilized plants may have a P/N ratio that considerably exceeds 0.15. We have measured P concentrations in plants in excess of 10 g kg^{-1} dry matter, and plants actually exhibit evidence of P toxicity. In these instances, the P/N ratio exceeds 0.15 and is of little use in predicting nutrient requirements.

The P/N ratio may change with the age of the plant. In young plants, the ratio may be less than it is in older plants. This, of course, indicates that young plants are more susceptible to P shortage, while older plants may exhaust the supply of nitrogen later in the growing period. This accounts for the well-established agronomic practice of placing fertilizer P near the seeds so that it is immediately available to young plants. Determining the P/N ratio of young plants can be useful for assessing the P status of the soil relative to its N status.

In their analysis of the growth of several crop plants grown under nutrient limiting conditions, van Keulen & van Heemst (41) showed that the concentration of the limiting element in tissue reached a characteristic limiting value. Using a procedure first described by de Wit (9), they provided a quantitative description of the relationship between production and nutrient supply based on two correlations: that between total uptake of the nutrient element and yield, and that between application rate of the element and uptake by the crop. By determining both uptake of an element and yield one can evaluate whether dry matter production is limited by the element under consideration or whether some other growth factor is in short supply. If the element is limiting, data points fall along a straight line where the slope is determined by the minimum concentration of the element, and concentration does not change as yield increases. Dry matter accumulation increases in direct proportion to the total uptake of the element in question. The relationship between application rate and uptake is usually linear for N and K, indicating that uptake follows first-order kinetics. This approach is based on ideas similar to those first expressed by Macy (27) when he attempted to quantify the mineral requirements of plants. He stated that "the sufficiency of a nutrient is a function of its percentage content in the plant." His central concept was that there is a "critical percentage" of each nutrient in the plant above which "luxury consumption" occurs and below which there is "poverty adjustment" until a "minimum percentage" is reached. Macy considered the critical nutrient composition to be an inherent or "ideal" nutrient composition of a plant. In maize, van Keulen & van Heemst (41) show that the concentration of N in the

grain is about 9 g kg^{-1} , and in the stover about 6 g kg^{-1} dry matter. For optimum maize grain production, however, both Stanford (40) and Grove (20) found that about 12 g N kg^{-1} of aboveground dry matter at physiological maturity was required. The values of van Keulen & van Heemst are consistent with Macy's minimum percentage, while those of Stanford and Grove are consistent with his critical percentage concept. We believe, therefore, that the concept of limiting concentration of an element does not hold over the entire response range of agricultural crops but that Macy's views expressed in the old paper still seem as valid as when they were first presented in 1936.

Little data on dry matter production and nutrient concentration is available for natural systems. The data of Peres et al (33) from the cerrado of Brazil, however, show that the concentrations of the elements they measured were similar in cerrado and in cerrado vegetation, with concentrations of 0.6 g P kg^{-1} and 8.5 g N kg^{-1} of litter material in both samples. Little variation in concentration was found from year to year. The minimum concentrations of P and N in the native annual grasses of the Sahel, reported by de Wit's group, were very close to those reported for the cerrado vegetation. This is evidence that both of these natural systems were nutrient limited in their native state.

CONCLUSIONS

Characteristics and properties vary as widely in tropical soils as in soils of other regions. The term "tropical soils" is of little use other than to identify the latitudes in which they occur. Highly weathered soils are more common in the tropics than in temperate regions. This prevalence results from the geological stability of tropical landscapes over long periods, especially in South America and Africa, and from the excessive rainfall that is common throughout much of the tropics. Highly weathered Oxisols, Ultisols, and Alfisols cover approximately 50% of tropical land areas. Oxisols and Ultisols are highly acidic, low in bases and plant nutrients, and frequently dominated by Al^{3+} in the subsoils. Tropical Alfisols are also acidic, but have more bases and less Al^{3+} than Oxisols and Ultisols.

Soil-plant interactions are consistent with expectations based on experience in the temperate region. Some interactions are more common in the tropics than in other regions, due to the prevalence of highly weathered soils and the intermittent distribution of rainfall. Water limitation is common not only during seasonal droughts but also during rainy seasons when a hostile soil environment limits root proliferation. Aluminum commonly restricts root growth, which prevents efficient use of soil-water and nutrients. Frequently, an inadequate supply of Ca^{2+} also restricts root growth, especially on Oxisols. Soil reserves of P, S, and K are typically low and potentially limiting.

The predominant soil orders of the tropics are characterized by clays of variable charge, and at unamended soil pH, their cation retention capacities are extremely low. Alfisols are generally well supplied with bases. The Ultisols and Oxisols, however, contain only small quantities of bases, much of which are contained in the vegetation. If the bases contained in the vegetation are lost, the soil supply is so small that little remains to be recycled. Correction of soil acidity increases the capacity of these soils to retain bases because cation retention capacity increases as pH increases, toxic ions such as Al^{3+} , Fe^{3+} , and Mn^{2+} are reduced, and microbial activity is enhanced. Many indigenous species apparently have sufficient tolerance to Al^{3+} that they at least survive on these soils. Much effort has been devoted to selecting agricultural plants tolerant of Al^{3+} . With the scarcity of Ca^{2+} in the rooting zone, this effort may well fail even though the roots are tolerant of Al^{3+} .

Nutrient limitations to plant growth in native systems are poorly documented by direct evidence. Investigators have employed various analyses to derive indirect evidence of general soil fertility or specific nutrient limitations. Phosphorus is commonly thought to limit the production of tropical forests and savannas. The de Wit group used fertilization experiments in the native grasslands of the Sahel and demonstrated that these systems were both N and P limited. Nutrient ratios, i.e. P/N, appear to be helpful in identifying individual nutrient limitations to growth, but such ratios must be used with care. Fertilizer trials are employed routinely with agricultural crops to determine nutrient availability and limitation. Forest fertilization, especially with N, is common in temperate regions but to our knowledge has not been attempted on native ecosystems in the tropics. Nutrient enrichment or fertilization experiments may be appropriate for evaluating nutrient limitations in terrestrial ecosystems.

A model looking at progressively more stringent limitations to growth provides a useful framework for analyzing plant nutrient limitations. De Wit's group demonstrated that native grasslands in the Sahel were more limited by nutrients than by water. We think it likely that semiarid systems are commonly nutrient limited and only become water limited when nutrient limitations are removed. In order to understand such complicated systems, we must use models and experimental approaches to address the fundamental chemical and biological processes in soils as well as the physiology and ecology of the plants.

ACKNOWLEDGMENT

This paper was prepared within the programs of the Center for Root-Soil Research and Tropsoils at Cornell University.

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